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Final Report

GROWTH OF CORALLINACEAE ON THE COAST OF MAINE

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INTRODUCTION

The crustaceous corallines are an important group of plant fossils in some Cenozoic and late Mesozoic limestones. It is the author's contention that the best use of these plants as stratigraphic and paleoecologic indicators can be made on the basis of extensive knowledge of both the living and the fossil forms. This report is about studies of the living New England crustaceous corallines, the first of a series of investigations planned of living and fossil members of the group. It is hoped that some of the work described here will eventually lead to generalizations of value in paleoecology, and that the structural and systematic observations will make for more accurate attempts to work out the evolutionary history of the fossils and also to apply this information to time stratigraphy.

In dealing first with the New England corallines, the study has been necessarily restricted in the number of genera and species treated, and the more massive types found in other regions, particularly the tropics, have not been available. However, by working initially in this area, it has been possible to treat a group of species in some detail with limited funds and equipment. Free diving, which has been used in this work for collecting and investigating the ecology of growing plants in situ, has proven to be a significant advance in technique over the traditional mode of working by dredge.

SUMMARY OF PROGRESS

During the summer and fall field seasons of 1960 and 1961, many thousands of specimens of crustaceous corallines were selected from a variety of habitats along the New England coast from Long Island Sound to southwestern New Brunswick. Much of the material has been retained as a working reference collection, while the anatomy and reproduction of over 300 individual plants has been investigated by microtome sectioning. An undescribed species (tentatively Phymatolithon rugulosum) and a species new to New England (Crodelia orbiculatum) have been found as important elements of the coralline flora.

From these collections it has been possible to work out a general depth and geographic distribution pattern for most of the species involved.

The area south of Cape Cod has not yet been surveyed in this study as much as northeastern New England. However, it is believed that what has been found is characteristic at least of the area between Nantucket Sound and eastern Long Island Sound. South of Cape Cod, Phymatolithon laevigatum and to a much lesser extent Lithothamnium lenormandi are important as rock encrustors. From the lower intertidal pools downward to the limit of the rocky bottom collected over in the area (about 50 feet below low water), these form thin crusts (commonly 0.5 mm thick) on ledges,cobbles, and small pebbles. On pebbly bottoms where there is a strong current, Phymatolithon laevigatum is frequently found completely coating pebbles to a thickness of a few millimeters. Both of these species extend north of Cape Cod. However, P. laevigatum is much less dominant in this area, decreasing in abundance northeastward along the coast and with a tendency to be restricted to mid-depths (about 15 to 40 ft below low

water). In this study, Lithothamnium lenormandi has been found only in the lower intertidal zone (in small pools and on bare ledges) in central and northern New England. Even in this restricted habitat it is usually sporadic and tends to be masked by the northern species.

In Massachusetts Bay, several rock-encrusting corallines are abundant which were not found south of Cape Cod. These include Clathromorphum circumscriptum, a plant primarily of lower intertidal pools and shallow water (0-20 ft b.l.w.), Lithothamnium laeve, an encrusting deep water coralline (30-85? ft), and L. glaciale, a branching, crustaceous type. This latter species apparently ranges from shallow to deep water. However, this range may be the result of species lumping, as will be discussed later. In this area, the encrusting corallines are certainly a more conspicuous element of the flora than they are south of Cape Cod. However, except for Clathromorphum circumscriptum, which in tide pools may form crusts 1-2 cm thick, these occur mostly as thin coatings a few millimeters thick on rocks, mussels, and gastropods.

Northeastward from Cape Ann and along the Maine coast, Cl. circumscriptum remains the most conspicuous crustaceous coralline in the lower tide pools and at shallow depths. In this area crusts of 2-3 cm thick are not unusual in the tide pools and specimens 5-6 cm thick have been found. In general, crusts and branches of Lithothamnium glaciale are better developed in this area, plants commonly reaching 1-2 cm in thickness in shallow water. In deeper water, L. laeve crusts, although of about the same thickness as those found in central New England, are much more abundant.

However, there are a number of important additional species which first appear in northern New England. Crodelia orbiculatum occurs as occasional

scattered plants on the north side of Cape Ann. Northeastward it becomes more and more an element in the coralline flora, and east of Mt. Desert Island, it becomes the most characteristic coralline of mid-depths. Although crusts of Cr. orbiculatum are mostly relatively thin (2-4 mm), in far eastern Maine it often occurs on boulders and cobbles almost to the exclusion of all other algae.

At Cape Neddick, on the southern Maine coast, the southernmost specimens of Clathromorphum compactum and Phymatolithon rugulosum were found. P. rugulosum forms relatively thin crusts (1-3 mm) in shallow to mid-depths, while Clathromorphum compactum occurs in mid-depths as hemispherical individuals reaching 2-3 cm in thickness and 5-8 cm in diameter. Both of these species become increasingly abundant eastward along the Maine coast.

Lithothamnium foecundum, a crustaceous coralline of mid- to deep water, has been found at only two localities along the coast: Mt. Desert Rock and Isles of Shoals. In both areas, which lie offshore from the coast, the plants occurred in abundance. This is primarily an arctic species (S. Lund, The Marine Algae of East Greenland, Copenhagen, 1959).

Epiphytic, crustaceous corallines belonging to the genera Dermatolithon and Fosliella are sporadically abundant in quite shallow water along the entire coast. They have not been studied carefully enough to warrant generalizations of distribution at the present time, but will be so treated during the coming months.

ANATOMICAL STUDIES

A detailed anatomical study of many of the New England species has brought

to light a number of previously undescribed features. Crustaceous corallines are generally recognized as bearing a weakly calcified single-celled surface layer (deck or cover cells) which are cut off upwards from the immediately underlying meristem cells. In this regard, they are unusual among red algae which with rare exceptions show apical growth of filaments.

In the thinner and probably shorter-lived epiphytic types, apparently only a single set of deck cells is formed. However, this study has shown that at least in some of the thicker, long-lived New England crusts, e.g., Lithothamnium glaciale, the Clathromorphums and the Phymatolithons, these cells are continuously divided off upwards and are released, providing the plants with a means of keeping their surfaces free from other organisms. This characteristic is especially marked in Lithothamnium glaciale, because in this species the cover cells are released in sheets rather than individually and are often elevated with the formation of the new layer below. Also, in this species, the cover cells are rectangular in section and are quite thick-walled. In this regard, they are distinct from all the other local species, and even the smallest fragment from the upper part of the thallus is determinable. In the members of the other genera mentioned, the surface cells are apparently dislodged individually. Cover cells in crustaceous corallines are usually described as lacking chromatophores. This is true of most of the New England species. However, it should be noted that this is a secondary feature: the young cover cells do bear chromatophores, and these later degenerate. A peculiar situation described by Suneson in Crodelia orbiculatum is a layer of cover cells 2-4 cells thick. These are normal, however, in that they lose their chromatophores progressively as they

are pushed upward. The result is a thin, chalky pellicle on the surface of the plant.

Clathromorphum circumscriptum and Cl. compactum bear very peculiar cover cells. In these species, the cover cells are normal in their position above the meristem, a lack of cell fusions, and an apparently thick inner wall. However, they bear abundant chromatophores and form a layer that, in a fully developed plant, ranges from about five to fifteen cells. The cover cells in this case form the chief photosynthetic layer, or "epithallium"; in cells cut off below the meristem, the chromatophores degenerate rapidly.

Asexual conceptacles in Clathromorphum are developed quite similarly to those in Lithothamnium; the meristem directly forms both the sporangia and the intermingled and surrounding sterile filaments. Foslie, however, originally set up Clathromorphum on the basis of its sunken conceptacles, and the manner in which the conceptacle roofs broke out. Later he combined the genus with Phymatolithon (defined essentially simply as having sunken conceptacles). Later authors have often discarded both of these genera, noting that there is a wide and essentially continuous range of conceptacle submergence in various lithothamnia. The present study indicates that the latter is probably a reasonable position, since the conceptacle depth in the thallus is a function of the relative rates of growth of the conceptacle primordia and the surrounding vegetative tissue. In Clathromorphum, the relative growth rates of these two tissues are nearly equivalent, essentially the same condition as found in the local Lithothamnium glaciale. The conceptacles are deeply sunken in Clathromorphum because of the overlying epithallium, and it is the cutting off of the epithallial cells over the conceptacle roof at maturity that produces the pecul-

iar "point-like" shallow hole described by Foslie. Only three species of importance have been placed in Clathromorphum. Two of these occur in New England. The third, Cl. loculosum, occurs in the Arctic Ocean and in the northern Pacific. A specimen of this species from the north Pacific and originally determined by Foslie was sectioned. Here the same distinctive meristem with thick overlying epithallium also appears. Thus it is tentatively proposed that the genus Clathromorphum be redefined, with the deep meristem and overlying epithallium as chief characteristics. Kylin ("Entwicklungsgeschichtliche Florideenstudien," Lunds Univ. Årsskrift, NF., Avd. 2, Vol. 24, 1928) described a somewhat analogous situation in Melobesia membranaceum, a vegetatively single-layered (plus cover cells), epiphytic lithothamnion. In this case, where the thallus around the conceptacles is oligostromatic, the divisions apparently occur in the basal layer. But the hypothallium-perithallium of Melobesia and Clathromorphum are quite different.

Pit connections between daughter cells are characteristic of Florideae. Their nature is much debated and is probably variable. Some of the New England crustaceous corallines possess pits showing opposing, densely staining, thin plates in the adjacent cells, as in Clathromorphum, Crodelia orbiculatum and in the epiphytic species. However, in all the New England species of the genera Lithothamnium and Phymatolithon, these pit "plates" are distinctly spherical and are generally quite large. The "plate" of the upper cell is typically larger than that of its lower neighbor.

Scattered vegetative cells of Phymatolithon laevigatum, especially those of the upper perithallium, possess a large, darkly staining body of unknown

nature. This has been found only in this species among the New England corallines, and is quite useful in identifying fragments of the plant.

REPRODUCTIVE STRUCTURES

Some of the New England corallines produce their reproductive structures only during certain seasons of the year. Clathromorphum and Phymatolithon are quite distinct in this regard; the conceptacle primordia appear in October or early November and the spores are released from the mature conceptacles in January and February. In C. compactum and P. rugulosum, only bisporic, asexual conceptacles have been found. In Cl. circumscriptum and P. laevigatum tetraspores and male plants occur rarely, but as yet no female plants have been found. Prior to this study, no sexual plants had been found in Clathromorphum, though Cl. loculosum commonly bears tetraspores. A normal sexual-asexual cycle has been described in Phymatolithon polymorphum, which in this study has not yet been found in New England waters.

It has been possible to describe the development of the asexual conceptacles of these four species from material collected during this study. The development in Clathromorphum and its similarity with Lithothamnium has been mentioned. The Phymatolithon species studied here and P. polymorphum as studied by Suneson ("The Structure, Life History and Taxonomy of the Swedish Corallinaceae," Lunds Univ. Årsskrift, N.F., Avd. 2, Vol. 39, No. 9, 1943) show a peculiar formation of the conceptacle primordia. Although the meristem, in the case studied here, lies in the typical position below a single or sometimes two cover cell layers, the conceptacle primordia are formed along a cup-like

surface extending deeply into the thallus. As the conceptacle develops, the overlying tissue is cut off and forms the white disks and spots characteristic of these species. The final conceptacles are thus normally deeply sunken. The genus Phymatolithon was originally set up on the basis of the sunken nature of the conceptacles. As mentioned for Clathromorphum, this relationship has commonly been disregarded in recent years. Thus it is tentatively proposed that the genus Phymatolithon be redefined, with the peculiar position and shape of the conceptacle primordium as the major characteristic.

Lithothamnium laeve bears its reproductive organs, sexual and asexual, during the summer. It is planned to investigate the development of these structures during the coming spring, a season not yet worked in the field in this study. From the mature material collected during the summer on the New England coast, it has been found that the mature cystocarp of L. laeve possesses a fragmentary fusion cell with apparent secondary pits between the fragments. Since secondary pits have previously been described only in the vegetative cells of two genera of the Lithophyllum group, it is desirable to study this matter in the developing female organs this spring. Also, in this species, the strongly thickened and plug-like upper wall of the sporangium (which eventually forms the pores of the asexual conceptacle) is lined by dense, heavily staining cells possibly having a secretory function. These are not found in other New England lithothamnia and are not known to have been described in the literature, although the drawings of some previous authors suggest that these might be present in other species.

The number of spores (normally seen from the surface and referred to as

pores) in each asexual conceptacle, and the size of the conceptacle, are commonly used as species-characterizing feature in lithothamnia. In the species discussed above, for example, Clathromorphum circumscriptum, Cl. compactum, Phymatolithon laevigatum, and Ph. rugulosum can be distinguished on the basis of these, among other features. As a general rule, in the species studied, spore number and conceptacle size are directly related. This feature is important when two closely related species overlap in their spore-count distribution. A preliminary survey of these features with regard to geographical distribution has been undertaken on Lithothamnium laeve collected along the New England coast. There is an apparent increase in asexual conceptacle size and in the number of spores per conceptacle northward. There are, however, some anomalies: for example, Isles of Shoals shows a collection with a very high count. But this is one of the two areas bearing the more northern species L. foecundum. It is planned to investigate this matter more thoroughly during the coming summer. More material and especially exact information on the depth of occurrence of individual plants is desirable. During the spring some of the Clathromorphum and Phymatolithon species will also be investigated in this regard.

Crodelia orbiculatum appears to be very unusual in the production of its reproductive organs. The sexual structures are produced in the summer, while the asexual organs are developed in the late fall.

The branching corallines are taxonomically a very difficult group. Many species were originally set up entirely on the basis of superficial characteristics, especially the form of the branching. Yet it has always been quite

apparent that ecology and substratum are important factors determining the superficial form of a plant. The New England branching, crustaceous corallines collected in this study are very similar anatomically. In section, they are easily distinguishable from all other corallines in the area and have been treated in preliminary work as Lithothamnium glaciale. A further study of anatomy and structure of the reproductive organs is now underway of the mass of branching coralline material that has been collected. It is possible that species are being lumped together. The collected, branching corallines of this region are all asexual and appear to reproduce without regard to season. However, this may be a taxonomic problem as discussed above.

GROWTH RATE

No reliable information is available about the growth rates of these plants. Such information would be valuable in estimating the length of time required for these organisms to form modern and ancient structures. To gain information on growth rates and to learn something about the essentially unknown early structural development of these plants, numerous underwater field stations with glass receiving plates have been set in appropriate areas during the times of spore release. By collecting these periodically, it is possible to work out initial growth rates and early development.

Clathromorphum circumscriptum has already been investigated in this regard. By this means and from year classes seen on relatively clear substrata, the following growth rate has been found in plants growing in 10-15 ft of water on exposed areas in eastern Maine. Spores after settling develop into

sporelings in January. These are about 100 μ in diameter and 25 μ in thickness; by July they will have reached 800 μ x 200 μ; the following July they would be about 6 mm x 600 μ; and the first asexual conceptacles are produced that fall when the plants are almost two years old. It must be remembered that these are average figures for exposed plants, and as in all settling and growth problems a normal type distribution with overlapping year classes could be expected from randomly selected plants. The young spore of this plant enlarges four to six times in volume after release from the parent conceptacle. After settling it is single-celled and is completely encased by a thick wall. Division proceeds inside of the wall, the spore being divided vertically into four or sometimes five segments. Division proceeds with little or no enlargment of the spore case until a basal layer of about 150 cells is produced. At this point, the central cells are two to three times larger in diameter than the peripheral cells and this condition remains throughout the life of the plant. Such a plant is typically two to three cells thick centrally, one cell thick at the margin. Eventually, upward growth of the plant ruptures the spore case along the basal margin. The marginal cells then grow outward developing into the hypothallium.

In addition to continued and more detailed examination of the above species, stations have been placed to collect spores of Phymatolithon laevigatum, Ph. rugulosum, Lithothamnium glaciale, and Clathromorphum compactum. These are now settling (February) and some have already been collected, but back-identification of the spores must wait until next summer when the young plants have reached a size large enough to permit identification. It is hoped

that Lithothamnium laeve can also be treated in this regard during the late spring and summer.

As has been discussed, Clathromorphum compactum, a plant of mid-depths along the northeastern part of the New England coast, is a well-defined fall spore producer. The spores are released from the conceptacles each year in mid-winter. The old conceptacles in this species are buried in the crust by continued upward growth during the spring. The final result in an old plant, which has essentially a hemispherical habit, is a series of zones of old conceptacles, each marking the addition of a year's growth to the thallus. In a number of crustaceous corallines "tissue layers" can be discerned in section. These layers are defined by changes in cell size and wall thickness. Also, in some cases, e.g., the New England Clathromorphum species, an apparent cessation of growth in the winter results in a heavily stained wall layer which, with apparent breaks, forms a minutely irregular hemispherical surface throughout the plant. In Clathromorphum compactum these tissue layers correspond exactly to the conceptacle layers. In some plants, portions of tissue, sometimes with parts of conceptacles, may break off at the time of spore production. New upward growth of the perithallium occurs at these breaks if they are not too deep. If they extend approximately to the base of the conceptacle perithallium re-growth may not occur. A new overgrowing hypothallium is then developed from the laterally undisturbed perithallium. These irregularities can sometimes produce quite an irregular pattern. However, the seasonal reproduction of the plant leaves little doubt about the nature of the layers. A few plants bearing irregularities have been studied in great detail in section. The results

quite distinctly indicate a series of continuous layers corresponding with the old conceptacles or their remains. A few plants from different depths from the same area show a decrease in growth rate with depth. This ranges from 500 μ per year (centrally in the plant) in plants collected at 20 ft b.l.w. to about 250 - 300 μ per year at 40 ft b.l.w. The relationship has not yet been studied in enough plants from different localities to allow drawing generalizations.

In recent years, a relationship between temperature and the amount of magnesium replacing calcium in the calcite lattice has been shown for some calcified marine organisms. While a relatively large body of information has been accumulated on the magnesium percentage in some groups of crustaceous corallines (tabulated by J. Harlan Johnson, Limestone—Building Algae and Algal Limestones, Colorado School of Mines, 1961), the relationship between magnesium percentage and latitude is much too vague to be used in paleoecological studies. Attempts to show a seasonal cycle of magnesium percentage in individual coralline crusts have also been essentially unsuccessful (Chave, K. F.,"Aspects of the Biochemistry of Magnesium. 1. Calcareous Marine Organisms," Jour. Geol. 62, 266-283, 1954). The above discussed studies on Clathromorphum compactum have indicated that this plant, if properly cut and prepared, should show an annual cycle of magnesium percentage, if disposition of this is a function of temperature. Plants of Cl. compactum, with anatomical information and directions for cutting were sent to Professor Chave at Lehigh University with a request for a magnesium analysis. The results obtained by Bradner Wheeler, one of his graduate students, using X-ray diffraction methods, show a striking

and consistent sine-like variation of magnesium with depth from the surface of the plant (between 10% and 14% of carbonate). The period of this curve corresponds exactly with the layers described from microscope sections.

PLANS FOR COMPLETION OF THE NEW ENGLAND STUDY

The author has elected to continue his field study on the New England coast until September, 1962. Although the development of the reproductive organs of species bearing these during the fall has been under investigation, it is necessary in some species to collect during the spring to follow the reproductive development. Also, a large number of stations bearing glass plates and slides have now been placed, and it is expected that it will be possible to work out growth rates and early development for other species, in addition to Clathromorphum circumscriptum. These are settling and being collected at the present time (February, 1962). It should be possible to work with other species in the late spring and early summer in the same way.

It is intended to increase the number of collecting sites along the coast. This is desirable to obtain more detailed ecological observation on the coralline flora in general and to investigate more closely geographical gradients such as conceptacle size, spore counts, and growth rates in the species already studied and in additional species. In the past, the work has been especially directed to the rock-encrusting corallines. The few New England species of coralline epiphytes will be investigated more closely during the next seven months. Also, it is planned to extend the collecting into the Bay of Fundy

and the southeastern coast of Nova Scotia. From the few collections obtained in this area during the past summer, it is expected that this will shed some light on taxonomic problems in the difficult branched species.

Most of the microscopic investigation described in this report has been undertaken on decalcified material. It is planned to make a series of ground sections in parallel with the decalcified material, beginning this spring. This is desirable to investigate characteristics of the calcified parts of the cell wall in an attempt to correlate them with the information already obtained.

The Department of Geology of the Massachusetts Institute of Technology has made some very limited funds available to the author for the continuation of this work until mid-June, 1962. The amount to be received, however, is not enough to complete the work already in progress, and additional support is needed. It is planned to close this phase of the research in September and report the detailed results at that time.